Received: 7 March 2022 | Accepted: 13 August 2022 | Published online: 26 October 2022

DOI: 10.1002/csc2.20838

Crop Science

ORIGINAL RESEARCH ARTICLE

Plant Genetic Resources

Comparative phenomics of root architecture and anatomy in *Phaseolus* species

Anica Sandra F. Massas[1] | **Christopher F. Strock**[1] | **Hannah M. Schneider**[1] | **Daniel G. Debouck**[2] | **Kathleen M. Brown**[1] | **Jonathan P. Lynch**[1]

[1]Dep. of Plant Science, The Pennsylvania State Univ., University Park, PA 16802, USA

[2]Genetic Resources Program, Centro Internacional de Agricultura Tropical, AA 6713, Cali, Colombia

Correspondence
Jonathan P. Lynch, Dep. of Plant Science, The Pennsylvania State Univ., University Park, PA 16802, USA.
Email: JPL4@psu.edu

Assigned to Associate Editor Valerio Hoyos-Villegas.

Funding information
United States Agency for International Development, Grant/Award Number: Feed the Future Innovation Laboratory for Climate Resilient Beans; National Institute of Food and Agriculture, Grant/Award Number: Project PEN04582; McKnight Foundation, Grant/Award Number: Collaborative Crop Research Program

Abstract

Phaseolus species are globally important food security crops. Drought and low soil fertility are primary constraints to *Phaseolus* production in developing nations. Root phenes have important roles in soil resource capture and plant performance. We profiled root phenotypes in 30 wild and seven domesticated *Phaseolus* taxa in laboratory and greenhouse environments. Our results reveal that substantial variation for root phenotypes exists among and within *Phaseolus* taxa, notably for phenes such as basal root number, basal root whorl number, root hair length, root hair density, metaxylem vessel number, and total cross-sectional area. Wild taxa display greater genetic variation for root architecture and anatomy and possess desirable phenotypes that are either not found or are not sufficiently expressed in domesticated accessions. Consequently, wild taxa represent an important resource for breeding programs to improve abiotic stress tolerance. Root phenotypes were also associated with the environment in the region of origin, suggesting that they have adaptive value. We speculate that significant variation in root phenotypes across different *Phaseolus* species is related to their abiotic stress tolerance and are valuable for breeding programs focused on improving edaphic stress tolerance.

1 | INTRODUCTION

Phaseolus is an American genus of approximately 80 species, mainly distributed in the tropics and subtropics (Porch et al., 2013). *Phaseolus vulgaris* L., or common bean, is an important source of protein and nutrients in many developing countries (Pachico, 1989). Of the 80 different species, *P. vulgaris* is considered the most important as a food security crop, although tepary bean (*P. acutifolius* A. Gray), scarlet runner bean (*P. coccineus* L.), lima bean (*P. lunatus* L.), and year bean (*P. dumosus*) also have agricultural significance (Debouck, 1999). The wide distribution and adaptation of beans to different environments contribute to the dramatic phenotypic variability that exists within the *Phaseolus* genus.

This diversity in wild *Phaseolus* germplasm can serve as a valuable resource for breeding programs to improve the environmental stress tolerance of domesticated varieties (Debouck, 1999; Nabhan et al., 1986), where wild accessions may possess valuable phenes that are not expressed in domesticated materials (Porch et al., 2013; Rao et al., 2013). For example, wild species such as *P. angustissimus*,

Abbreviations: LDA, linear discriminant analysis; TCSA, total cross-sectional area.

P. acutifolius, and *P. filiformis* are adapted to the arid and semiarid environments of the southwestern United States and northwestern Mexico, and exhibit relatively high levels of tolerance to drought, salinity, and heat stress (Balasubramanian et al., 2004; Bayuelo-Jiménez et al., 2002; Beebe et al., 2013). Tepary bean (*Phaseolus acutifolius*) accessions have been used in breeding programs as a source of drought and heat tolerance (Rao et al., 2013), as well as for resistance to common bacterial blight, leafhoppers, and bruchids (Singh et al., 1998). Similarly, wild *Phaseolus vulgaris* accessions with tolerance to low soil fertility and adaptation to higher latitudes have been introgressed with cultivated lines with agronomically desirable seed size, color, and growth habit (Acevedo et al., 2006; Acosta-Gallegos et al., 2007; Blair et al., 2006, 2016; Cortés et al., 2013; De Ron, 2015; Kipe-Nolt et al., 1992; Kornegay & Cardona, 1991; Kornegay et al., 1993; Rodriguez et al., 2016; Shellie-Dessert & Bliss, 1991; Singh, 2001). Even where there are limitations in prebreeding efforts to introgress wild material with cultivars, the identification of phenes that confer tolerance to abiotic stress in this exotic material can still serve as a model for recombining traits in more elite germplasm. Despite this success in utilizing diversity from wild germplasm in breeding programs, further characterization and understanding of phenotypes that drive abiotic and biotic stress tolerance in wild *Phaseolus* taxa is crucial.

Common bean production throughout much of the world is characteristic of smallholder producers, often on marginal soils with limited use of inputs. Consequently, biotic and abiotic stresses represent major constraints to both subsistence and commercial production (Miklas et al., 2006). Most prominently, soil fertility and drought are primary limitations to the productivity of these agroecosystems. Given the root system is directly responsible for the acquisition of soil resources, understanding adaptive strategies for the capture of soil resources is essential to improving abiotic stress tolerance. The divergence in spatiotemporal availability of multiple soil resources makes the optimization of root growth for plant fitness dependent upon the predominant edaphic stress in each environment. For example, in drought prone environments where the soil dries from the top down through evaporation and water uptake by crops, the greater availability of water in deeper horizons necessitates a strategy of deep foraging by the root system (Lynch, 2013). Contrastingly, environments with nutrient poor volcanic soils (Andosols), or weathered mineral soils (Oxisols, Utisols, some Alfisols) require foraging strategies that exploit the topsoil where the availability of immobile resources like phosphorus are most abundant (Lynch, 2019).

Architecture is one organizational scale of the root system that can determine the effectiveness of soil foraging in a given environment by modifying the placement of roots in soil domains where growth limiting resources are most available.

Core Ideas

- Significant variation in root architecture and anatomy exists among wild and domesticated bean taxa.
- Taxa from different geographic origins have distinct root phenotypes.
- Wild taxa express novel diversity for root phenotypes and may serve as genetic resources for breeding programs.

In *Phaseolus* species, root architectural phenes that affect soil foraging depth include basal root growth angle (Bonser et al., 1996; Fenta et al., 2014; Liao et al., 2001; Liao et al., 2004; Miguel et al., 2015; Rangarajan et al., 2018; Rubio et al., 2003; Ge et al., 2000), basal root whorl number (Basu et al., 2007; Miguel et al., 2013; Rangarajan et al., 2018), adventitious root number (Miller et al., 2003; Ochoa et al., 2006; Rangarajan et al., 2018; Walk et al., 2006), and lateral root branching density (Rangarajan et al., 2018). In common bean, greater basal root whorl number (Miguel et al., 2013), shallower basal root growth angles (Miguel et al., 2015), and production of adventitious roots (Miller et al., 2003) are associated with greater shallow root length distribution and subsequently greater topsoil foraging, which is important in phosphorus-limited environments (Lynch & Brown, 2001). Contrastingly, deeper basal root growth angle and less allocation to root classes foraging the epipedon can improve the capture of mobile, deeply distributed resources like water and nitrate (Strock et al., 2021).

Although root architecture affects the placement of roots in the soil, root anatomy regulates the metabolic cost of soil exploration, the penetration of hard soil domains, the axial and radial transport of water, and interactions with soil biota including mycorrhizal fungi, pathogens, insects, and the rhizosphere microbiome (Lynch et al., 2021). Anatomical phenes that reduce the metabolic cost of soil exploration can serve to enhance the capture of both mobile and immobile nutrients (Lynch, 2018). For example, under low phosphorus availability, secondary growth of roots is suppressed, affording greater allocation of resources to total root length rather than radial thickening, thereby facilitating greater exploration of soil domains where resources are more abundant (Strock et al., 2018). Root hairs are subcellular outgrowths of epidermal cells and are another anatomical phene that expand the volume of soil foraged in the rhizosphere. Root hairs have been shown in modeling and empirical studies to benefit the capture of immobile nutrients like phosphorus (Bates & Lynch, 2000a; Gahoonia & Nielsen, 1998; Miguel et al., 2015) as well as mobile resources like water (Carminati et al., 2017), and nitrogen (Saengwilai et al., 2021), while incurring little metabolic cost (Bates & Lynch, 2000b). Xylem vessels are another anatomical feature that are responsible for the bulk of axial transport of water and nutrients through the root system. Variation in the diameter and number of xylem vessels affects root hydraulic conductivity and has been shown to influence water use and plant productivity under drought stress (Klein et al., 2020; Lynch, 2018; Lynch et al., 2014; Purushothaman et al., 2013; Strock et al., 2021).

Presently, classification of *Phaseolus* taxa is entirely based on morphological, physiological, agronomic, and molecular characteristics of the aboveground tissue (Singh et al., 1991). Nevertheless, *Phaseolus* species may also exhibit distinct features in roots at the architectural or anatomical scales that afford some specific ecological adaptation across the geographic distribution of this genus. In the present study, our goals were to test the hypotheses that (a) significant variation in root phenotypes exists among *Phaseolus* taxa, (b) the geographic origin of these species has a significant effect on soil foraging strategies, and (c) soil foraging strategies differ between domesticated and wild *Phaseolus* taxa.

2 | MATERIAL AND METHODS

2.1 | Plant material

Fifty-two entries representing 30 *Phaseolus* species (*P. acutifolius*, *P. angustissimus*, *P. augusti*, *P. carterae*, *P. costaricensis*, *P. debouckii*, *P. dumosus*, *P. filiformis*, *P. glabellus*, *P. grayanus*, *P. hintonii*, *P. leptostachyus*, *P. lunatus*, *P. maculatus*, *P. macvaughii*, *P. magnilobatus*, *P. marechalii*, *P. micranthus*, *P. microcarpus*, *P. montanus*, *P. novoleonensis*, *P. oligospermus*, *P. pachyrrhizoides*, *P. pedicellatus*, *P. rotundatus*, *P. talamancensis*, *P. tuerckheimii*, *P. vulgaris*, *P. xanthotrichus*, and *P. zimapanensis*) and seven entries representing domesticated genotypes of five species (*P. acutifolius*, *P. coccineus*, *P. dumosus*, *P. lunatus*, and *P. vulgaris*) were obtained from the International Center for Tropical Agriculture (CIAT), Cali, Colombia (Supplemental Table S1). The *Phaseolus* taxa were selected based on their geographical distribution and ecological adaptation, and are endemic to regions throughout Mexico, Peru, Bolivia, Argentina, Guatemala, Colombia, the United States, and Costa Rica.

2.2 | Laboratory phenotyping

Seeds were surface-sterilized for 1–2 min with 0.5% (v/v) NaOCl in water, rinsed with deionized water, mechanically scarified with sandpaper and germinated in rolls of brown germination paper (Number 78, Anchor Paper Company). Five seeds of each accession were rolled up in each sheet of germination paper representing a single replicate. The rolls were placed upright in 2-L beakers containing 0.5 L of 0.5 mM $CaSO_4$. The beakers were filled with 10 rolls and wrapped with cellophane punctured with small holes to maintain humidity and provide aeration. The beakers were placed in growth chambers for seed germination for 5 to 6 d in darkness at 28 ˚C. The seedlings were the transferred to a growth chamber for 14 d at 30 ˚C and 16 h of light (Philips 27242–7 F30T12/CW/RS T12 Fluorescent Lamp, 130 μmol m^{-2} s^{-1}). After 14 d, roots were carefully removed from the germination paper and three representative seedlings were evaluated from each replication. The number of basal roots and basal root whorls were counted, and roots were then stored in 75% ethanol (v/v) for subsequent analysis of root hairs.

2.3 | Greenhouse phenotyping

The greenhouse experiment was conducted under controlled conditions at the Pennsylvania State University, University Park, PA, USA (40° 85′ N, 77° 82′ W), from March to May 2013. Seven domesticated and 45 wild taxa (Table S1) were planted in the greenhouse. Seeds were germinated as described above. Seedlings were transplanted into 6.5-L containers (bottom diameter 17 cm, top diameter 20.5 cm, depth 21.5 cm), with media comprised of 40% sand, 40% vermiculite, and 20% perlite. Genotypes were planted in a completely randomized design with four replications per accession. Nutrient solution was supplied to pots through the irrigation system, consisting of 1.5 mM KNO_3, 1 mM $Ca(NO_3)_2$, 0.25 mM $MgSO_4$, 0.0625 mM $(NH4)_2SO_4$, 0.375 mM $NH_4H_2PO_4$, 50 μM KCl, 25 μM H_3BO_3, 2 μM $MnSO_2$, 2 μM $ZnSO_4$, 0.5 μM $CuSO_4$, 0.5 μM $(NH_4)_6Mo_7O_{24}$, and 50 μM Fe-NaEDTA. The pH of the nutrient solution was adjusted every other day to 5.5 to 6.0 with KOH and HCl.

Destructive sampling was conducted at 6 to 7 wk after planting. Data collected in the greenhouse experiment included number of adventitious roots, basal root branching, basal root length, basal root growth angle, shoot dry weight, basal root whorl number, basal root number, and taproot length. The number of adventitious roots, basal roots, and basal root whorls were determined by counting. Dry weights were determined from tissues dried at 60 ˚C for 72 h. Root lengths and branching were determined by imaging the washed root system on an EPSON Perfection V700 PHOTO scanner and quantifying the scanned images using WinRhizo software (WinRhizo Pro, Régent Instruments). Roots were then stored in 75% ethanol (v/v) for subsequent analysis of root anatomy and root hairs.

2.4 | Root hair quantification

Root hair length (mm) and root hair density (number of root hairs per mm^2 of root surface area) were determined in basal root segments sampled from behind the root tip in the zone of root hair maturation. Representative basal root segments were briefly stained with Toluidine Blue O (0.05% w/v in water) for better visualization with a light microscope (Nikon SMZ-4). Images of root hairs were captured with a Nikon DS-Fi1 camera at 40x magnification using NIS-Elements F2.30 software. An image of a Hemocytometer (Hausser Scientific) was taken along with the root hair image for scale. ImageJ (http://rsbweb.nih.gov/ij/download.html) was used to measure root hair length and density in images from five representative root segments per replication.

2.5 | Root anatomical phenotyping

For analysis of root anatomy, two, 2-cm-long root segments from the greenhouse trial were excised from basal roots behind the root tip in the zone of root hair maturation. The samples were gradually dehydrated in ethanol series (75, 85, 90, and 100% ethanol, v/v), then preserved by critical point drying (Leica EM CPD300). Dried root segments were sectioned using laser ablation tomography to obtain images for anatomical analysis (as described in Hall et al., 2019; Strock et al., 2019a). Anatomical features including total cross-sectional area, xylem area, and xylem number were measured from these images of root cross sections using MIPAR software (MIPAR.beta.8). Theoretical axial metaxylem conductance (k_h; kg m MPa^{-1} s^{-1}) was calculated for each root cross-sectional from measurements of xylem vessels using the modified Hagen Poiseuille law (Equation 1), where d is the diameter of the vessel in meters, ρ is the fluid density (equal to water at 20 °C; 1,000 kg m^{-3}), and h is the viscosity of the fluid (equal to water at 20 °C; 1×10^{-9} MPs s^{-1}; Tyree & Ewers, 1991).

$$k_h = \left(\frac{\pi\rho}{128\eta}\right)\sum_{i=1}^{n}\left(d_i^4\right) \quad (1)$$

where k_h is the theoretical axial metaxylem conductance.

2.6 | Data collection and analysis

All statistical analyses were performed using R 3.6.2 (R Core Team, 2016). Prior to all statistical tests, normality and homoscedasticity of the data were determined using the Shapiro–Wilk test and the nonconstant error variance test, respectively. Where data did not meet these assumptions, a Box–Cox or log transformation was used to help normalize the data. Significant correlations and differences for all data analyses were considered at $\alpha \le .05$.

Allometric analysis was performed according to Niklas (1994) to provide insight into the differential growth rates of shoot biomass vs. root phenes. The slope of the regression line of the log transformed shoot biomass with log transformed root phenes signifies the scaling coefficient (α). Isometry is recognized according to the scaling exponent (0.33 for linear dimension phenes and 0.67 for area phenes). Scaling exponents near these values indicate isometric or proportionate growth of that phene with respect to biomass.

Pearson's correlation analysis was used to determine the relationships among root phenes (tradeoffs and allometry). Principal component analysis was used in the identification of phenes that help to distinguish origins. Unsupervised cluster analysis (K-means) was used to determine if origins have unique aggregates of root phenes. Linear discriminant analysis was used to determine if taxa from the driest environments and taxa from the wettest environments could be differentiated based on root phenotypes. Analysis of variance and Tukey's honest significant difference (HSD) was used for comparison of root phenes across clusters, rainfall groups and latitude bins.

2.6.1 | Principal component and unsupervised cluster analyses

Principal component analysis was conducted using adventitious root number, adventitious root length, adventitious branching, basal root number, basal branching basal root length, basal root growth angle, primary root length, primary branching, primary root diameter (diameter), root hair density, root hair length, xylem vessel area, xylem vessel number, hydraulic conductance, and root total cross sectional area (TCSA).

To determine if accessions from different geographic origins have unique aggregates of root phenotypes, K-means cluster analysis was performed across all accessions using the genotypic means of each root phene. Root phenes used in this analysis included adventitious root number, adventitious root length, adventitious branching, basal root number, basal root branching, basal root length, primary root length, primary root branching, basal root growth angle, taproot diameter, root hair density, root hair length, xylem vessel area, xylem vessel number, hydraulic conductance, and root TCSA. Within group sum of squares was used to determine the optimal number of cluster assignments across all the accessions. Pearson's χ^2 test of independence was then used to explore the distribution of accessions from each geographic origin across the clusters ($N_{ARG} = 1$, $N_{BOL} = 2$, $N_{COL} = 1$, $N_{CRI} = 6$, $N_{GTM} = 6$, $N_{MEX} = 29$, $N_{PER} = 3$, $N_{USA} = 4$). Comparisons of root phenotypes for accessions assigned to each cluster were made using analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test.

2.7 | Linear discriminant analysis

To further understand if taxa from different environments could be differentiated by root phenotypes, linear discriminant analysis was performed on groups of taxa from similar latitudes or annual rainfall. Taxa were binned by the annual rainfall of their location of origin into five groups: 0 to 499 mm ($n_{0\text{-}499} = 11$ taxa), 500 to 999 mm ($n_{500\text{-}999} = 20$ taxa), 1,000 to 1,499 mm ($n_{1,000\text{-}1,499} = 8$ taxa), 1,500 to 1,999 mm ($n_{1,500\text{-}1,999} = 7$ taxa), and 2000+ mm ($n_{2,000+} = 5$ taxa). Taxa were also binned by latitude into six groups: 24˚S to 5˚S ($n_{24\text{-}6S} = 6$ taxa), 5˚N to 10˚N ($n_{5\text{-}10N} = 7$ taxa), 14˚N to 17˚N ($n_{14\text{-}17N} = 9$ taxa), 18˚N to 20˚N ($n_{18\text{-}20N} = 10$ taxa), 21˚N to 25˚N ($n_{21\text{-}25N} = 14$ taxa), and 30˚N to 33˚N ($n_{30\text{-}33N} = 5$ taxa). Root phenes used in this analysis included adventitious root number, adventitious root length, adventitious branching, basal root number, basal root branching, basal root length, primary root length, primary root branching, basal root growth angle, taproot diameter, root hair density, root hair length, xylem vessel area, xylem vessel number, hydraulic conductance, and root TCSA.

TABLE 1 Basal root number, basal root whorl number, root hair density, and root hair length of all measured taxa in the greenhouse (root age 7 wk) and roll-ups (root age 14 d). Data shown are means ± standard error (SE). Means are the average of four replications and means with the same letters are not significantly different ($p \leq .05$) as determined by a Spearman Rank correlation (r) test performed within each phene

Phenes	Location	Mean	SE	Spearman rank correlation (*r*)
Basal root number	Roll-ups	5.2a	0.44	.7***
	Greenhouse	5.3a	0.64	
Basal root whorl number	Roll-ups	1.5a	0.1	.8***
	Greenhouse	1.7a	0.2	
Root hair density	Roll-ups	341.6a	47.1	.2*
	Greenhouse	250.6b	32.3	
Root hair length	Roll-ups	1.4a	0.1	.17*
	Greenhouse	0.53b	0.04	

*Significant at the .05 probability level. ***Significant at the .001 probability level.

3 | RESULTS

3.1 | Wild and domesticated groups vary in architectural and anatomical phenes

Wild and domesticated groups varied in anatomical and architectural phene states. In this context we highlight four species represented by both wild and domesticated taxa: *P. acutifolius*, *P. dumosus*, *P. lunatus*, and *P. vulgaris*. Domesticated types of *P. vulgaris*, *P. acutifolius*, and *P. dumosus* had greater numbers of basal roots and basal root whorls when compared with wild types (Figure 1a, c).

Among all 52 entries, domesticated taxa had significantly greater basal root number and basal root whorl number than wild taxa (Figure 1b, d). Root hair length and density showed substantial variation among taxa but not between domesticated and wild groups (Figure 2). *P. coccineus* showed the greatest root hair length among the domesticated taxa, and *P. filiformis* and *P. tuerckheimii* had the greatest root hair length among wild taxa (Figure 2a). Domesticated *P. acutifolius* exhibited the greatest root hair density among all domesticated taxa (Figure 2c).

The number of metaxylem vessels displayed large variation among species and between domesticated and wild types, ranging from four to >140 vessels per cross-sectional area in the basal root (Figure 3). Domesticated *P. acutifolius* displayed the greatest metaxylem vessel number and metaxylem vessel area among all taxa (Figure 3a, c). Wild *P. montanus* and *P. costaricensis* had the greatest metaxylem vessel area and number compared with other taxa (Figure 3a, c). Domesticated taxa had a larger metaxylem vessel area and metaxylem vessel number compared with wild taxa (Figure 3b, d).

Total cross-sectional area of basal roots had large variation among all the taxa with a range of 0.2 to 3.7 mm^2. Wild *P. costaricensis* had the greatest TCSA (3.7 mm^2) and wild *P. magnilobatus* had the smallest TCSA (0.2 mm^2; Figure 4a). For the four taxa with both wild and domesticated accessions, wild *P. dumosus*, *P. lunatus* and *P. vulgaris* had greater cross-sectional area than domesticated accessions of these species (Figure 4a). Across all taxa, domesticated taxa had significantly greater TCSA compared with wild taxa (Figure 4b). Total axial hydraulic conductance ranged 800-fold among taxa (Figure 4c). Wild *P. acutifolius* (1.0×10^{-7} kg m MPa^{-1} s^{-1}) and *P. vulgaris* (8.9×10^{-8} kg m Mpa^{-1} s^{-1}), had the greatest hydraulic conductance among the wild taxa. *P. lunatus* showed the greatest conductance among the domesticated taxa (Figure 4c). Across all taxa, wild taxa had less hydraulic conductance compared with domesticated taxa (Figure 4d).

3.2 | There are differences in root phenotypes measured in greenhouse and roll-up environments

Growth environments affected phenotypic values. Root hair length was 158% greater in roll-ups than in the greenhouse (Table 1). Root hair density was 137% greater in the roll-ups than in the greenhouse (Table 1). Spearman correlation coefficients between greenhouse and roll-ups were low for root hair density and root hair length ($r = .20$ and $r = .17$) but were stronger between greenhouse and roll-up experiments

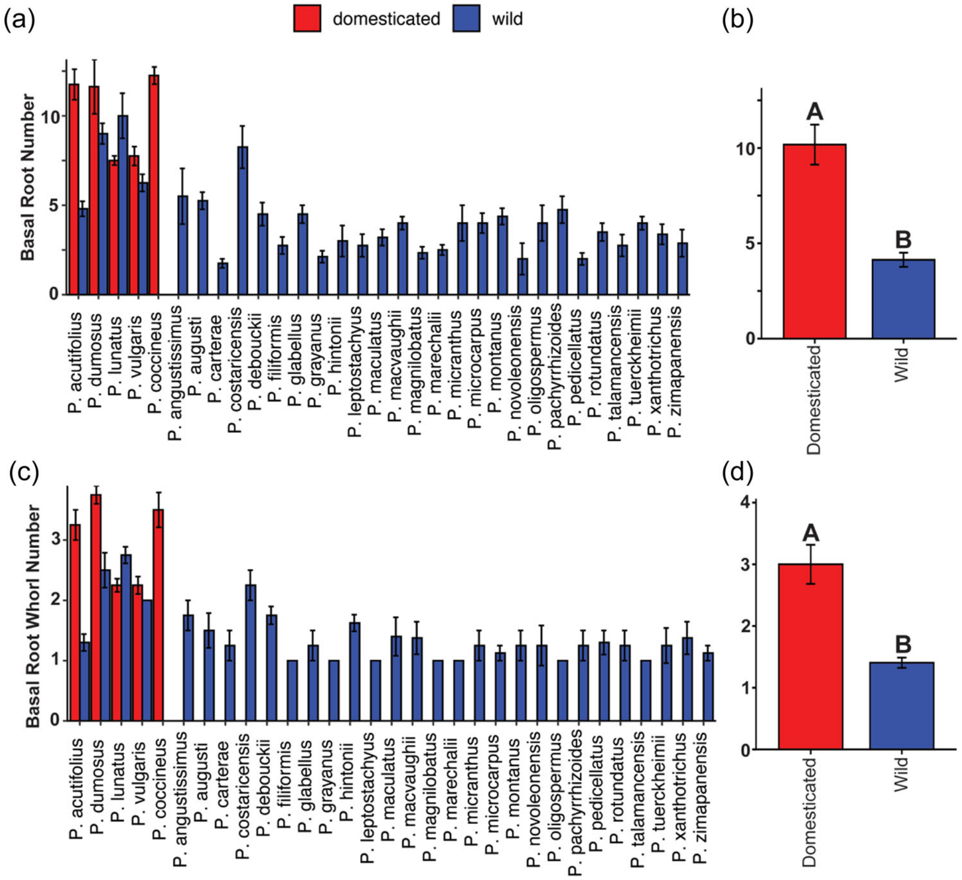

FIGURE 1 Genetic variation of basal root number (a, b) and basal root whorl number (c, d) of *Phaseolus* species and comparison between wild ($n = 30$) and domesticated ($n = 5$) taxa (b, d) in the greenhouse. Data shown are means ± standard error. Means are the average of four replications and means with the same letters are not significantly different ($p \leq .05$)

for basal root number and basal root whorl number ($r = .70$ and .80).

3.3 | Anatomical and architectural root phenes have allometric relationships to biomass

Most root phenes in wild taxa exhibited allometric relationships with shoot biomass and had larger scaling exponent values than the expected isometric values (Table 2; Supplemental Figure S1). Therefore, as shoot biomass increased, the proportional increase of these phenes would be greater than predicted with isometric growth (Table 2; Supplemental Figure S1). Total cross-sectional area and metaxylem vessel area, with scaling coefficients $\alpha > .67$, are positively allometric with shoot biomass, meaning the phene values increase faster than shoot biomass. In wild species, root hair density, and basal root growth angle scaled isometrically with biomass (Table 2). In domesticated species, basal root branching, basal root length, taproot branching, taproot diameter, and hydraulic conductance scaled isometrically with biomass (Table 2). Wild *P. dumosus* had the greatest mean shoot dry biomass (31.8 g), followed by domesticated *P. coccineus* and wild *P. lunatus*. Within *P. vulgaris*, the domesticated taxa had greater shoot dry biomass than wild taxa (Supplemental Table S3). In Mesoamerican *P. vulgaris*, the domesticated types had greater shoot dry biomass than wild taxa (Supplemental Table S3).

3.4 | Relationships exist between root phenotypes and environmental factors

Significant correlations were detected between root phenotypes and the annual rainfall and latitude of the location of origin for these taxa (Table 3).

3.5 | Taxa from similar origins have unique aggregates of root phenes

Principal component analysis was used to identify root phenes that distinguish taxa. The first two principal components accounted for 53.3% of the variability in the data set and

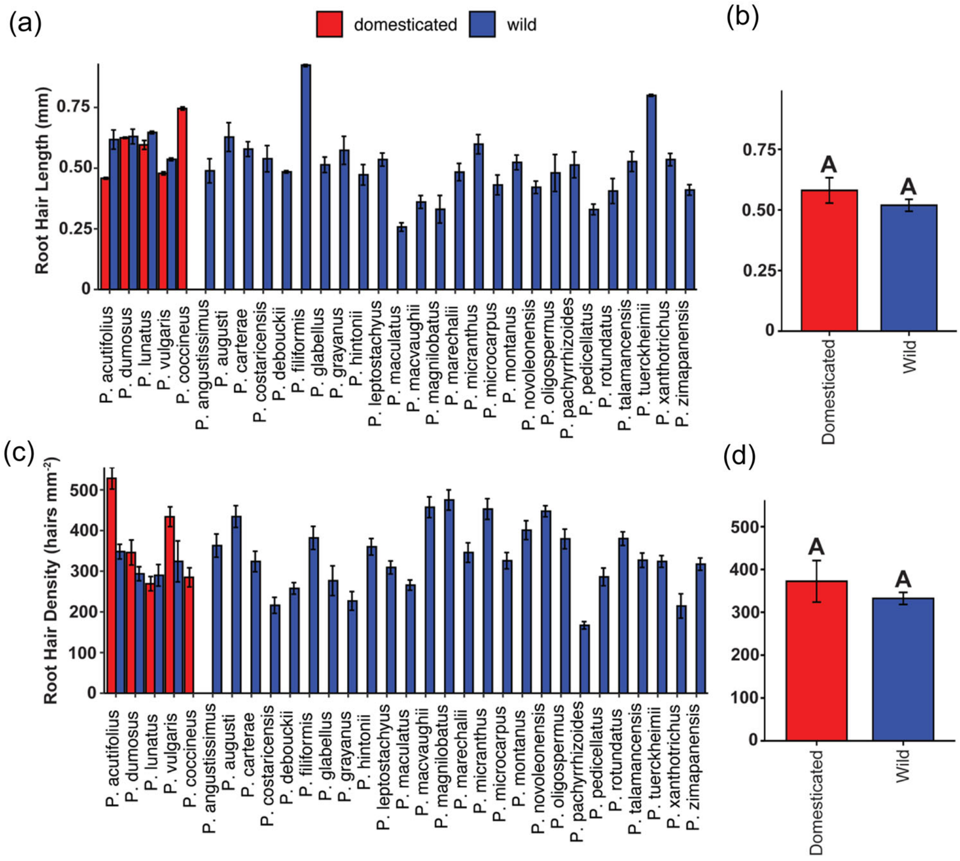

FIGURE 2 Genetic variation of root hair length (a, b) and root hair density (c, d) of *Phaseolus* species and comparison between wild ($n = 30$) and domesticated ($n = 5$) taxa (b, d) in the greenhouse. Data shown are means ± standard error. Means are the average of four replications and means with the same letters are not significantly different ($p \leq .05$)

were primarily influenced by branching density of all root classes and root anatomical phenotypes (Figure 5, Table 4). Principal component 1 (PC1) was most heavily influenced by branching of the basal and primary roots, whereas PC2 was loaded with xylem vessel attributes and root thickness (TCSA; Table 4). Distinct aggregation of taxa from different origins was observed when plotted across the first two principal components (Figure 5).

To gain further perspective on how taxa from different regions have unique aggregates of root phenes, unsupervised cluster analysis of root phenotypes was performed across all taxa (Figure 6). Analysis of within group sum of squares indicated that three clusters were optimal for unsupervised k-means cluster analysis. Pearson's χ^2 test of independence showed that taxa from different origins were asymmetrically represented across these three clusters ($\chi^2 = 24.484$, $p = .04$), suggesting that origins have distinct integrated root phenotypes (Figure 6). Cluster 1 was dominated by taxa of Argentinian, Colombian, Costa Rican, and Guatemalan origin, taxa from Bolivia and the United States were mostly aggregated in Cluster 2, whereas Peruvian taxa were mostly associated with Cluster 3. Taxa from Mexico were evenly represented across all three clusters. Analysis of variance and Tukey HSD (Figure 6) applied to data generated in the greenhouse indicated that Cluster 1 had root systems with short but dense root hairs, and a thick taproot with high conductance in comparison to Cluster 2. The cluster dominated by taxa from Bolivia and the United States (Cluster 2) had especially short and sparse root hairs and a root anatomy with xylem features producing a very low hydraulic conductance. Conversely, Cluster 3 that included Peruvian taxa had long root hairs and large hydraulic conductance capacity.

3.6 | Taxa from the driest environments and wettest environments can be differentiated based on root phenotypes

A linear discriminant analysis (LDA) model built using the taxa from areas with the greatest annual rainfall (2,000+ mm) and areas with the least annual rainfall (0 to 499 mm) yielded a 67% accuracy in assigning taxa to xeric or mesic environments on the basis of root phenotypes. In this model, taxa from the driest environments were effectively differentiated from taxa from the wettest environments by LD1 (Figure 7A),

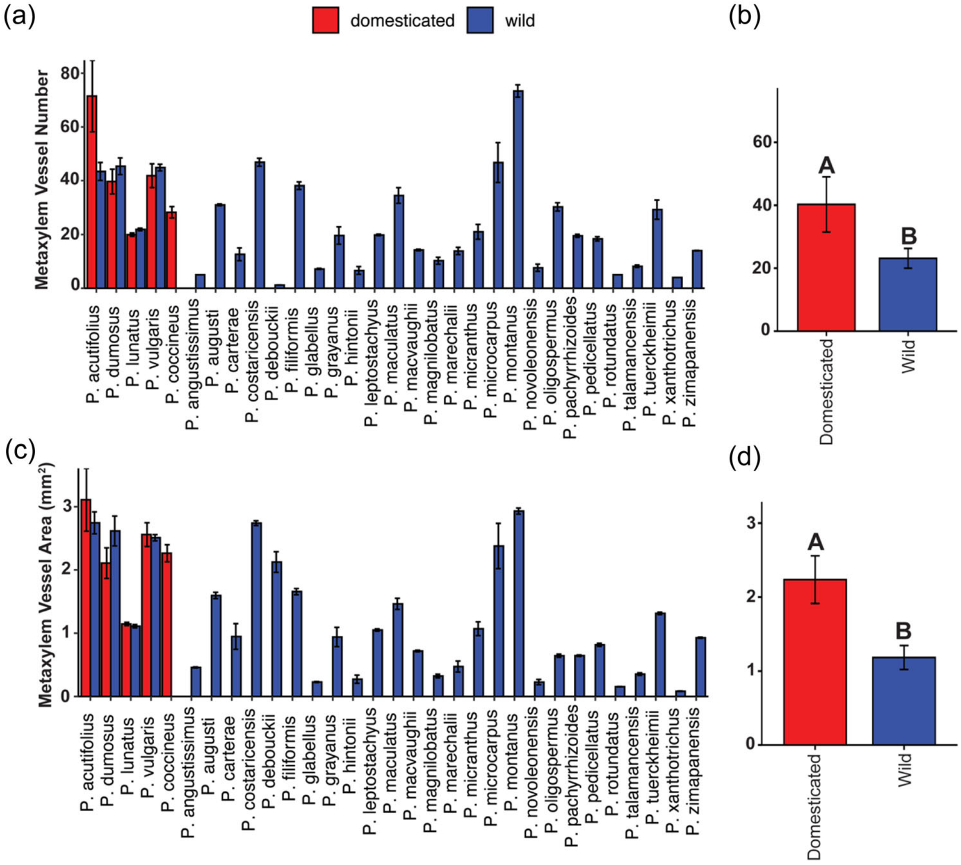

FIGURE 3 Genetic variation of metaxylem vessel number (a, b) and metaxylem vessel area (c, d) of *Phaseolus* species and comparison between wild ($n = 30$) and domesticated ($n = 5$) taxa (b, d) in the greenhouse. Data shown are means ± standard error. Means are the average of four replications and means with the same letters are not significantly different ($p \leq .05$)

which was most strongly influenced by adventitious branching, primary root length, root hair length, and root total cross sectional area (Table 5). Comparison of root phenes across all five rainfall bins using ANOVA and Tukey HSD suggested that taxa from some drier environments tended to have greater branching of basal roots, longer and thicker primary roots with greater xylem vessel area, and greater hydraulic conductance than taxa from some wetter environments (Figure 7). *Phaseolus* species from extremely dry climates have fewer adventitious roots than those from moderately dry climates.

Comparison of root phenotypes across latitude bins using ANOVA and Tukey HSD indicated that taxa from environments in the southern hemisphere (24˚S to 5˚S) had a low density of longer root hairs, longer and highly branched primary, basal and adventitious roots, a large number of basal roots, and a large hydraulic conductance capacity compared with temperate climatic zones in the northern hemisphere (Supplemental Figure S2). Those taxa coming from the more temperate climatic zone in the northern hemisphere had thicker, shorter roots with few laterals, few root hairs, shallow root growth angle, and smaller hydraulic conductance (Supplemental Figure S2).

4 | DISCUSSION

The present study provides a comprehensive representation of phenotypic variation for root architecture and anatomy in wild and domesticated accessions across diverse taxa of *Phaseolus*. We observed wide variation for root architectural and anatomical phenotypes within and among *Phaseolus* species, and specifically between wild and domesticated *Phaseolus* taxa (Figures 1, 2, 3, 4). In addition, geographic origin has large effects on root phenotypes within *Phaseolus* taxa (Tables 2, 3 Figures 5, 6, 7; Supplemental Figure S2). We noticed distinct aggregation of phenotypes among taxa from different origins (Figure 5). Considerable root phenotypic variation among *Phaseolus* taxa is expected considering the distribution of these accessions across a wide range of latitudes, precipitation patterns, and soil taxa. Population-specific variation for root architecture has been previously reported within *Phaseolus vulgaris* (Jochua et al., 2020; Strock et al., 2019b) and similarly, region-specific differences in root anatomy and architecture among this broader panel of taxa likely reflect adaptations to each species' endemic environment. Just as there are distinct differences in shoot morphology,

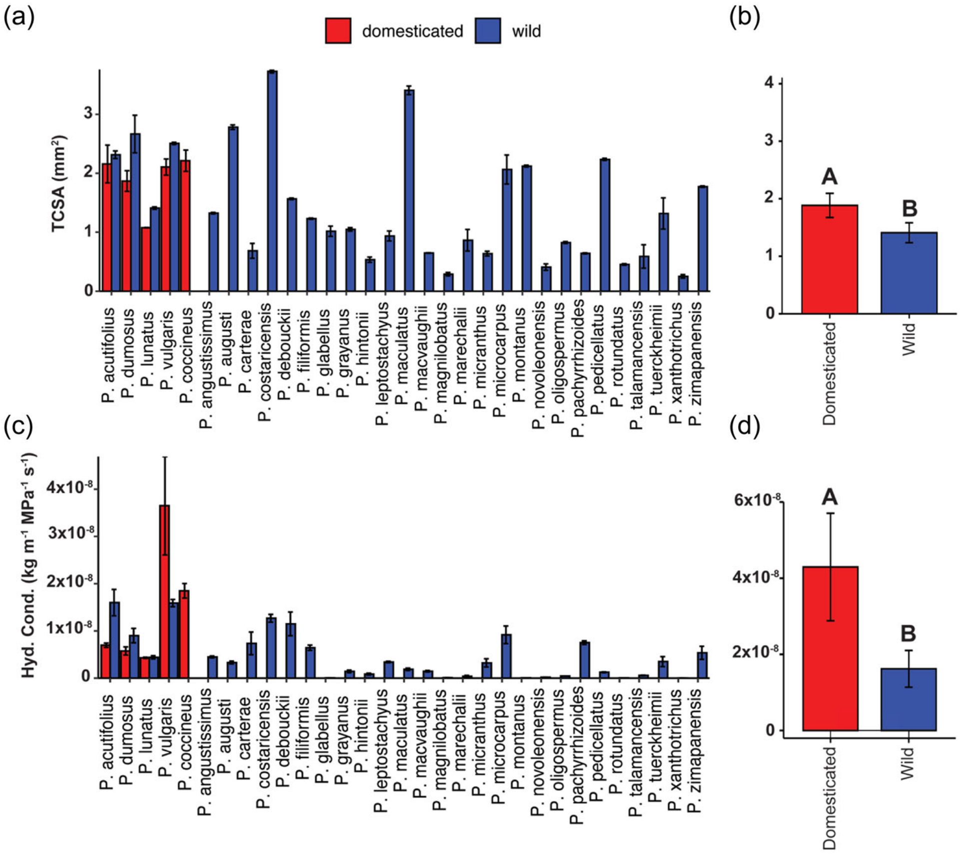

FIGURE 4 Genetic variation of total cross-section area (TCSA) and hydraulic conductance among 31 taxa (a, c) of *Phaseolus* species and comparison between wild ($n = 30$) and domesticated ($n = 5$) taxa (b, d) in the greenhouse. Data shown are means +/- standard error. Means are the average of four replications and means with the same letters are not significantly different ($p \leq .05$)

phenology, and molecular characteristics across these taxa, variation in root phenotypes would have emerged due to geographic separation of these groups and maintained over time by the self-pollinating nature of these species.

The divergence in spatiotemporal availability of soil resources across the geographic distribution of the *Phaseolus* genus results in tradeoffs in the value of root phenotypes that modify root system depth. Consequently, the observed variation in root phenotypes and foraging strategies across these taxa is likely driven by variability in growth limiting resources across environments. Root phenotypes that encourage shallow soil foraging reduce acquisition of resources that may exist in deeper regions of the soil profile and vice versa. For example, while shallow root systems are adaptive for taxa from environments limited by phosphorus availability or regions with sparse, intermittent rainfall, the distribution of roots in shallow soil domains would be detrimental to taxa from environments with terminal drought, leaching of key nutrients, or temperature extremes (Lynch, 2018). Therefore, preferential allocation to either shallow or deep root classes, coupled with positive feedback between root growth, soil exploration, and resource acquisition, can result in root phenotypes which tend to focus on either shallow or deep soil exploration (Burridge et al., 2020; Strock et al., 2019b). Although this strategy may be ideal in environments either predominately limited by either shallow or deeply distributed resources, it may be less optimum in environments with multiple constraints.

Because edaphic conditions in agronomically managed fields lie in sharp contrast with those of natural environments, root phenotypes that enhance acquisition of limiting resources in native soils are likely to be distinct from root phenotypes which optimize productivity in high input environments (Lynch, 2018; Lynch et al., 2021). Although many breeding programs make selections and develop new cultivars under well irrigated, highly fertilized conditions, wild taxa are subject to natural selection under multiple stresses, experience competition from a diversity of other species, and exist in soils with heterogeneous resource distribution. Consequently, as we observe in the present survey of root architecture and anatomy, wild taxa express novel root phenotypic variation and represent an excellent source of genetic material for breeding programs focused on the development of efficient, resilient crops.

We observed large differences in basal root number, basal root whorl number, and taproot length between domesticated

TABLE 2 Allometric comparisons of correlations between plant biomass and root phenotypes for wild and domesticated species. Advantageous root number (ARN), basal root number (BRN), basal root whorl number (BRWN), basal root branching (BRB), basal root length (BRL), basal root growth angle (BRGA), root hair density (RHD), root hair length (RHL), total cross-sectional area (TCSA), metaxylem vessel area (XVA), dry shoot biomass metaxylem vessel number (XVN), and Hydraulic conductance (Hydraulic Cond) were measured from the greenhouse (7 wk). Adjusted coefficient of determination (R^2), intercept (Int.), scaling coefficient (α), and p value (p) for the regression line are shown and significant relationship at $p \leq .05$

	Wild				Domesticated			
Phene	R^2	Int.	α	p	R^2	Int.	α	p
ARN	.08***	−0.24	1.51	≤.001***	.07	0.42	0.87	≤.05*
BRN	.42***	−0.93	1.75	≤.001***	.02	2.05	0.47	NS[†]
BRWN	.36***	−1.12	3.42	≤.001***	.08	2.5	0.52	NS
BRB	.12*	−1.1	2.11	≤.01**	.32*	−2.03	1.55	≤.001***
BRL	.45**	−1.23	1.87	≤.01**	.80***	−3.49	1.47	≤.001***
BRGA	.11	−2.12	1.23	NS	.17	−2.88	1.48	≤.01**
Taproot length	.62***	6.6	2.24	≤.001***	.28	2.25	0.22	NS
Taproot branch	.23**	−3.23	1.32	≤.01**	.40***	−4.5	2.44	≤.001***
Taproot diameter	.045***	3.32	−1.1	≤.01**	.028**	2.19	−0.12	NS
RHD	−.03	2.5	−0.11	NS	.33	3.03	0.02	NS
RHL	.30***	−0.76	6.21	≤.001***	.13	2.66	1.15	≤.05*
TCSA	.17*	0.87	1.16	≤.01**	.55	2.16	0.98	≤.05*
XVA	.40***	1.08	13.2	≤.001***	.001	3.01	1.71	NS
XVN	.31***	1.42	1.06	≤.001***	.29	2.87	0.09	≤.05*
Hydraulic Cond	.52***	5.5	0.54	≤.001***	.63***	2.91	0.14	≤.001***

*Significant at the .05 probability level. **Significant at the .01 probability level. ***Significant at the .001 probability level. †NS, nonsignificant.

and wild taxa, likely reflective of significant differences in soil resource availability and distribution between agriculturally managed and native soils (Figure 1). Wild taxa of *Phaseolus* have fewer basal roots and whorls compared with domesticated taxa (Figure 1, Table S2). In *P. vulgaris* and *P. acutifolius*, fewer basal roots have been associated with a deeper foraging strategy (Burridge et al., 2020; Strock et al., 2021). Because wild bean typically grows in regions where rainfall averages between 500 to 1,850 mm yr^{-1} and there may be little precipitation occurring after the plants flower, it is logical that some of the wild beans evaluated in the present study would have root systems that are adapted to seasonal drought (Debouck, 1989, 2000; Freytag & Debouck, 2002; Gentry, 1969). A study by Berny-Mier y Teran et al. (2019) found that wild accessions of the Mesoamerican gene pool in *Phaseolus vulgaris* were more drought tolerant than domesticated accessions from this same gene pool. Similarly, our observations of root architecture suggest that water is likely a key limitation for wild accessions in native soils and consequently, many wild *Phaseolus* taxa have a deeper foraging strategy that is adaptive to the acquisition of subsoil resources such as water.

In addition to root architectural phenotypes that are better suited for dry environments, wild bean taxa tend to have anatomical phenotypes that are more adapted to water-limited conditions compared with domesticated accessions. Specifically, many of the wild accessions generally display reduced metaxylem vessel number, metaxylem vessel area, and total cross-sectional area compared with the few domesticated varieties evaluated (Supplemental Table S2; Figures 3, 4). Under water-limited conditions, small-diameter metaxylem vessels would reduce the hydraulic conductance per vessel and may increase water use efficiency through a strategy of soil water banking, where a “low conductance” anatomy phenotype meters water extraction from the drying soil, thereby moderating desiccation of root tips and the surrounding rhizosphere for sustained soil exploration and water capture later in the season (Manschadi et al., 2006; Palta et al., 2011; Richards & Passioura, 1989; Vadez, 2014). The smaller xylem vessels in wild taxa would also be a benefit for roots in drier soils where negative tension on xylem vessels can be severe, leaving large diameter vessels more vulnerable than narrow vessels to dysfunction through cavitation (Hacke & Sperry, 2001; Tyree et al., 1994). In perennial dicot species, this hydraulic failure typically occurs in the roots, where xylem vessels are wider and longer than in shoots (Hacke & Sperry, 2001; Nobel & Jordan, 1983; Pockman & Sperry, 2000; Sperry & Ikeda, 1997; Sperry & Saliendra, 1994). In contrast, root anatomy with large diameter xylem vessels are generally adaptive in humid environments with sufficient water

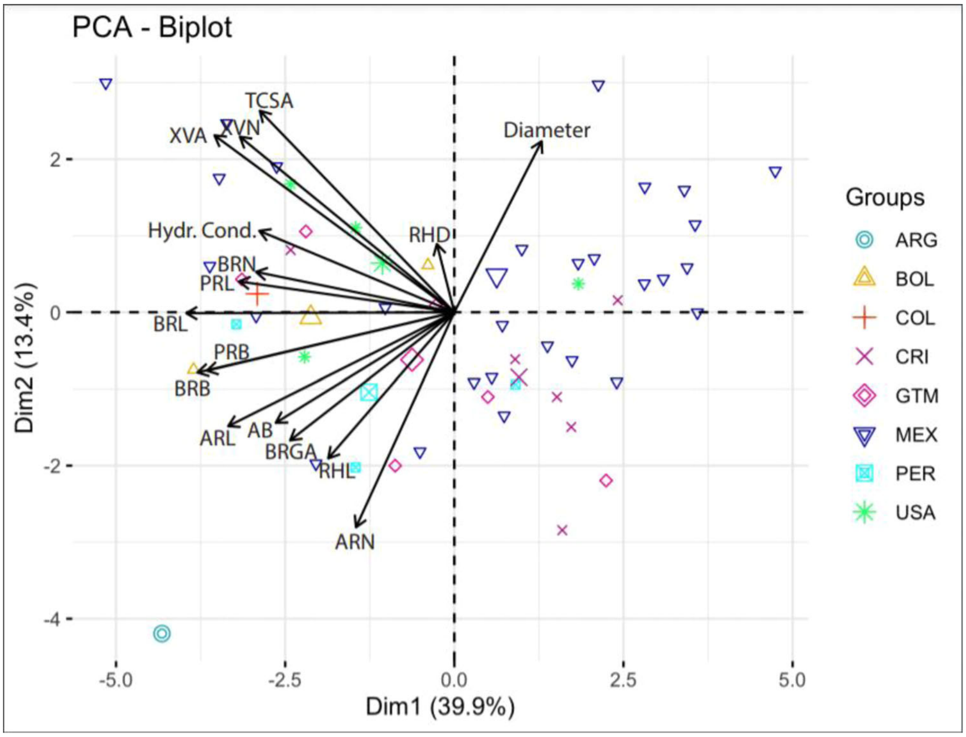

FIGURE 5 Biplot showing the distributions of origins across the first two principal components determined from a principal component analysis (PCA) of root phene evaluated in 51 taxa originating from North to South America. Plot shows separation of origins on the basis of root phenes. Root phenes include adventitious root number (ARN), adventitious root length (ARL), adventitious branching (AB), basal root number (BRN), basal branching (BRB), basal root length (BRL), basal root growth angle (BRGA), primary root length (PRL), primary branching (PRB), primary root diameter (diameter), root hair density (RHD), root hair length (RHL), xylem vessel area (XVA), xylem vessel number (XVN), hydraulic conductance (HydraulicCond), and root total cross sectional area (TCSA). $N_{ARG} = 1$, $N_{BOL} = 2$, $N_{COL} = 1$, $N_{CRI} = 6$, $N_{GTM} = 6$, $N_{MEX} = 29$, $N_{PER} = 3$, $N_{USA} = 4$. Origins include Argentina (ARG), Bolivia (BOL), Colombia (COL), Costa Rica (CRI), Guatemala (GTM), Mexico (MEX), Peru (PER), and the United States (USA)

availability and low risk of cavitation, allowing for maximum water and nutrient transport to support growth (Comas et al., 2013; Purushothaman et al., 2013; Strock et al., 2021; Tyree et al., 1994).

Although a reduced capacity for hydraulic conductance in many wild taxa can serve a soil water banking strategy for improved tolerance to drought, a few wild accessions from the driest environments had thicker roots with greater capacity for transport of water (Table 3). *Phaseolus acutifolius* is an example of a species endemic to dry regions and has the greatest metaxylem vessel number and area of all taxa surveyed (Figure 3, Table S4). In species like *P. acutifolius*, thick roots with large hydraulic conductance likely integrate with a deep distribution of root length to facilitate utilization of abundant water reserves at depth. Although xylem morphology affects the transport of water through the plant, access to water is dependent upon the distribution of roots throughout the soil profile, and consequently, xylem phenotypes have been shown to integrate with root architecture to affect water use strategies (Strock et al., 2021). Specifically, in *Phaseolus acutifolius*, a thick taproot with high conductance root anatomy integrates with root architecture that promotes deep distribution of root length in a strategy to exploit water reserves deep in the soil profile (Strock et al., 2021).

In contrast to these more traditional perspectives on the relationship between xylem vessels and water transport, recent work has suggested that xylem vessel vulnerability to cavitation is not the primary constraint on transpiration under drought, but rather the loss in soil hydraulic conductivity of the rhizosphere (Carminati & Javaux, 2020). In this context, the greater root hair length and density in some accessions may improve root to soil contact and promote continued water acquisition in drying soils (Carminati et al., 2017). Nevertheless, among the taxa surveyed in this work, rainfall was positively correlated with root hair length (Table 3). This trend might be explained by areas with greater precipitation being associated with more weathered, infertile soils. In environments with heavy rainfall, the loss of nutrients from surface runoff and leaching often serve as a major limitation to soil health (Yao et al., 2021). It has been shown that *Phaseolus* accessions with longer, denser root hairs have enhanced phosphorus acquisition in phosphorus deficient soil, and many of

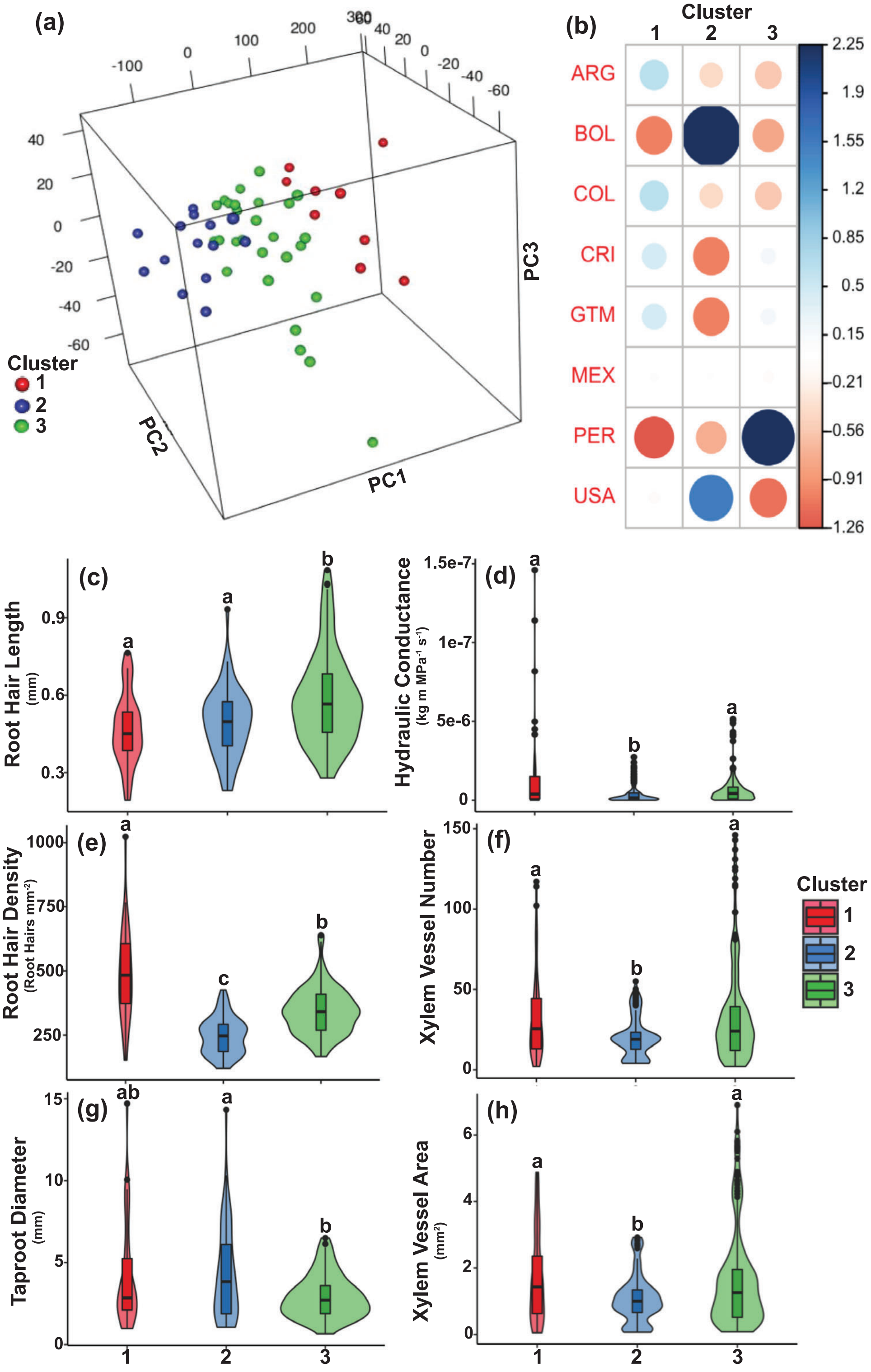

FIGURE 6 (a) Three-dimensional pseudo-principal component analysis (PCA) plot showing how clusters effectively separate from one another across the first three principal components. (b) Plot of residuals from Pearson's χ^2 test of the distributions of origins across clusters. Origins include Argentina (ARG), Bolivia (BOL), Colombia (COL), Costa Rica (CRI), Guatemala (GTM), Mexico (MEX), Peru (PER), and the United States (USA). Positive residuals in blue and negative residuals in red specify a positive and negative association, respectively, between a given origin and cluster. (c–h) Violin plots showing the median, interquartile range, 95% confidence intervals, and frequency of root phenes that are significantly different between clusters. For each phene, comparisons are made across the three clusters $n_1 = 72$, $n_2 = 120$, and $n_3 = 286$. Means within each panel with the same letter are not significantly different at $\alpha \leq .05$ as determined by Tukey's honestly significant difference test

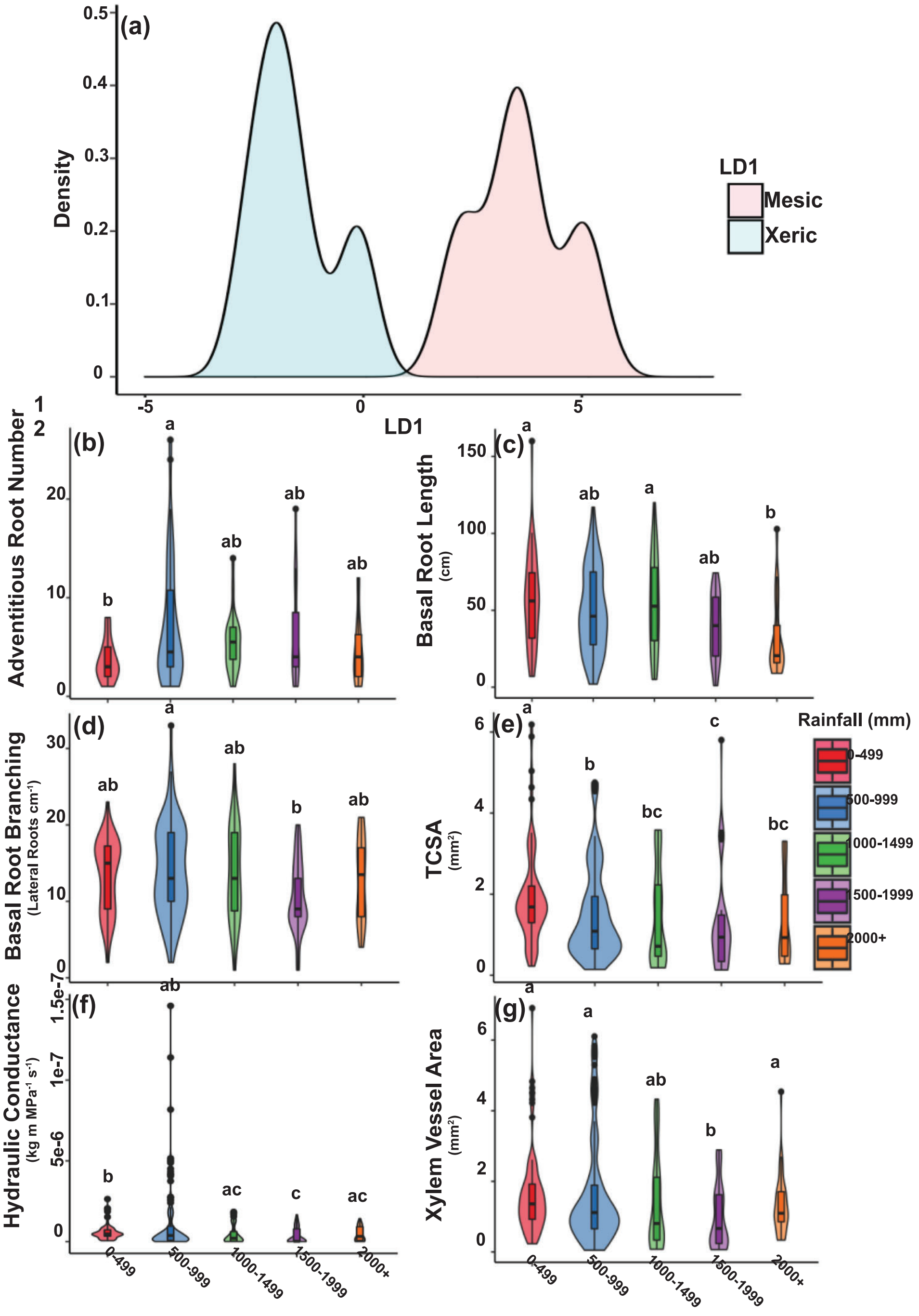

FIGURE 7 (a) Density plot showing the variation in discriminant function values for taxa coming from xeric environments (0–499 mm rainfall bin) and taxa coming from mesic environments (2,000+ mm rainfall bin). (b–g) Violin plots showing the median, interquartile range, 95% confidence intervals, and frequency of root phenes within all five rainfall bins. For each phene, comparisons are made across the five rainfall bins $n_{0\text{-}499} = 88$, $n_{500\text{-}999} = 160$, and $n_{1,000\text{-}1,499} = 64$, $n_{1,500\text{-}1,999} = 56$, $n_{2,000+} = 40$. Means within each panel with the same letter are not significantly different at $\alpha \leq .05$ as determined by Tukey's honestly significant difference test

the species displaying long root hair phenotypes are endemic to regions with soils that are volcanic in origin with inherently low phosphorus availability (Singh Gahoonia & Nielsen, 2004; Lynch, 2011).

Interestingly, the expression of root hair density and length differed between the greenhouse and roll-ups (Table 1), likely due to both environmental and developmental influences. Although the growth conditions were controlled in each environment, differences in the age of roots as well as other abiotic factors such as nutrient availability, moisture content, and mechanical damage during the washing process may influence root hair phenotypes (Nestler et al., 2016; Burak et al., 2021). Contrastingly, the number of basal roots and whorls were stable between measurements in seedlings and mature

TABLE 3 Pearson's correlation coefficients (*r*) of adventitious root number (ARN), basal root number (BRN), basal root length (BRL), basal root whorl number (BRWN), root hair density (RHD), root hair length (RHL), primary root length (PRL), taproot branching density (Tap RB), basal root growth angle (BRGA), dry shoot biomass, total cross-sectional area (TCSA), metaxylem vessel area (XVA), metaxylem vessel number (XVN), and Hydraulic conductance (Hydraulic Cond) with rainfall and latitude. Root phenotypes measured in the greenhouse (7 wk after planting) on all taxa studied

Phene	Rainfall	Latitude
	r	
ARN	−.01 ns[†]	−.33*
BRN	−.09 ns	−.19*
BRB	−.12 ns	−.25*
BRL	.24*	−.23*
BRWN	−.06 ns	−.17*
RHD	−.13 ns	.13 ns
RHL	−.12 ns	−.15*
PRL	−.15*	−.17*
Tap RB	−.05 ns	−.25*
BRGA	.06 ns	−.17*
Biomass	−.26*	−.14*
TCSA	−.16*	.04 ns
XVA	−.13*	.08 ns
XVN	−.17*	.11*
Hydraulic Cond.	−.12*	.15*

*Significant at the .05 probability level. [†]ns, nonsignificant.

plants, and Spearman rank correlations demonstrated that environment did not substantially alter the ranking of basal root number and basal root whorls among entries (Table 1). These results parallel previous reports of stability for measurements for basal roots measured in seedlings and mature plants grown in the field (Strock et al., 2019b), and that basal root number is not affected by soil variability (Miguel et al., 2013). Phenes like basal root number that can be observed early in plant development and are stable across environments would serve as excellent targets for direct phenotypic selection as phenotyping seedlings can be high throughput and require little investment of labor and resources compared with phenotyping mature, field-grown plants (Zhu et al., 2005; Vieira et al., 2007; Nestler et al., 2016; Strock et al., 2019b).

Although these relationships between individual root phenes are notable, broader understanding of soil foraging strategies is more appropriately conceptualized as the interaction among multiple root phenes that constitute an integrated root phenotype (York et al., 2013). These taxa exhibit distinct combinations of root phenes that may afford some specific ecological adaptation across their geographic distribution. Although trends in root phenotypes between the five rainfall groups were not always statistically detectable from comparisons using Tukey HSD (Figure 7b-g), LDA models suggested that taxa from the driest environments tended to have fewer adventitious roots, greater root branching, longer and thicker primary roots with greater xylem vessel area, and higher hydraulic conductance than taxa from wetter environments (Figure 7a, Table 5). As adventitious root number (Miller et al., 2003; Ochoa et al., 2006; Walk et al., 2006; Rangarajan et al., 2018), and root branching density (Rangarajan et al., 2018) have been shown to modify the depth of soil foraging, this model suggests that the integration of deep root architecture combined with high conductance anatomy may benefit annual dicots in drought prone environments.

Additionally, consideration of multiple root phenes in the principal component analyses showed that most of the variability across the taxa was in root branching density and root anatomy phenes (Figure 5, Table 4) and taxa from different origins could be differentiated by these phenotypes (Figures 5, 6b). Specifically, taxa from Argentina, Colombia, Costa Rica, and Guatemala had root systems with denser root hairs, and thicker taproots with xylem features producing high conductance in comparison to taxa from Bolivia and the United States (Figure 5). These taxa from Central and South America are likely more adapted to drought and low fertility soils than accessions from Bolivia and the United States.

Unsupervised cluster analysis grouped taxa from different geographic regions by their aggregate root phenotype (Figure 6). Cluster 2 composed mostly of taxa from Bolivia and the United States had xylem features with low hydraulic conductance and moderate root hair phenotypes, whereas Clusters 1 and 3 representing taxa from other regions of South and Central America had high hydraulic conductance and dense root hairs (Figure 6). The effective separation of taxa from different regions through unsupervised cluster analysis of their root phenotypes indicates a common strategy for soil resource foraging within these groups that may be related to their endemic environment.

The observed differences in root phenotypes between taxa and accessions from diverse geographic region provide further support for the theory that there is no single root phenotype that can be optimally adaptive across many environments (Dathe et al., 2016; Rangarajan et al., 2018; Strock et al., 2019b). The extent of variation that observed within and across taxa from similar environments supports the concept that different combinations of root phenotypes can achieve similar strategies for resource acquisition for a given environment. This has been previously exemplified through in silico work, where several root architectural phenotypes have been shown to similarly generate optimal fitness outcomes under P and N limitation (Dathe et al., 2016; Rangarajan et al., 2018).

TABLE 4 Loading scores for each root phene across the first three principal components (PC) used in K-means cluster analysis

	PC1	PC2	PC3
Adv. root number	−0.12618226	−0.419751817	−0.11927774
Adv. root length	−0.29014353	−0.222135145	−0.21426281
Adv. branching	−0.22907279	−0.215526653	−0.27541726
Basal root number	−0.25440257	0.078936342	0.47145919
Basal branching	−0.32951748	−0.117681309	0.01786464
Basal root length	−0.34374613	−0.001904915	0.26701491
Primary root length	−0.27621691	0.060216293	0.39516016
Primary branching	−0.31752596	−0.114224008	0.10015844
Basal root growth angle	−0.21068899	−0.249899678	0.10258096
Primary root diameter	0.11196263	0.334307178	0.34432447
Root hair density	−0.02244077	0.133453361	−0.31814212
Root hair length	−0.16178317	−0.285079135	0.09762570
Xylem vessel area	−0.30767265	0.345841162	−0.20078381
Xylem vessel number	−0.27512867	0.343285517	−0.22938767
Hydraulic conductance	−0.25022230	0.159195539	−0.25162519
TCSA	−0.24953109	0.393917166	−0.08866231

Note. Adv., advantageous; TCSA, total cross-sectional area.

TABLE 5 Coefficients for each root phene across the first linear discriminant in an analysis that was performed on groups of taxa from environments with similar annual rainfall

	LD1
Adv. root number	0.44925712
Adv. root length	−0.34912466
Adv. branching	1.29102781
Basal root number	−0.38622493
Basal branching	−0.31579721
Basal root length	−0.51270533
Primary root length	−1.11475691
Primary branching	0.49437909
Basal root growth angle	0.64109668
Primary root diameter	−0.04734793
Root hair density	−0.77035164
Root hair length	−1.73424963
Xylem vessel area	0.66911703
Xylem vessel number	−0.28186929
Hydraulic conductance	0.16611447
TCSA	−2.05066082

Note. Taxa were binned by being endemic to areas with greatest annual rainfall (2,000+ mm) and areas with the least annual rainfall (0 to 499 mm). Adv., advantageous; TCSA, total cross-sectional area.

5 | CONCLUSIONS

Understanding anatomical and architectural root phenotypes, and their interactions with each other and the environment will support the development of improved crop cultivars with enhanced water and nutrient acquisition. These results go beyond the conclusions of previous reports on root phenotyping not only by demonstrating taxonomic differences in individual root phenes, but by considering the broader soil foraging strategies of integrated root phenotypes among *Phaseolus* taxa. Our results reveal that substantial variation for root phenotypes exists among and within *Phaseolus* taxa, notably for phenes such as basal root number, basal root whorl number, root hair length, root hair density, metaxylem vessel number, and total cross-sectional area. Wild taxa display greater genetic variation for root architecture and anatomy and possess desirable phenotypes that are either not found or are not sufficiently expressed in domesticated accessions. Consequently, wild taxa represent an important resource for breeding programs to improve abiotic stress tolerance. Even where directly introgressing wild accessions with modern cultivars is challenging, the identification of phenotypes that confer tolerance to abiotic stress in this exotic material is helpful in developing breeding ideotypes. Root phenotypes were also associated with the environment in the region of origin, suggesting that they have adaptive value. We speculate that significant variation in root phenotypes across different *Phaseolus* species is related to their abiotic stress tolerance and are valuable for breeding programs focused on improving edaphic stress tolerance. Given that root architectural and anatomical phenotypes appear to be a defining characteristic of different taxa, further elucidation of various strategies from root phene aggregates would be a prime topic for targeted physiological studies, as well as genomic approaches with larger panels of domesticated and wild accessions. Additionally, genomic studies with both domesticated and wild populations of *Phaseolus* would be useful in further elucidating the evolution of the observed phenotypic variation in groups and geographic regions.

AUTHOR CONTRIBUTIONS

Anica Sandra F. Massas: Formal analysis, Investigation, Writing – original draft. Christopher F. Strock: Formal analysis, Visualization, Writing – review & editing. Hannah M. Schneider: Formal analysis, Writing – review & editing. Daniel G. Debouck: Writing – review & editing. Kathleen M. Brown: Writing – review & editing. Jonathan P. Lynch: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interests or personal relationships that could influence the work reported in this paper.

ORCID

Christopher F. Strock https://orcid.org/0000-0003-1432-8130

Jonathan P. Lynch https://orcid.org/0000-0002-7265-9790

REFERENCES

Acevedo, M., Steadman, J., Rosas, J., & Venegas, J. (2006). New sources of resistance to bean rust and implications for host-pathogen coevolution. *Annual Report of the Bean Improvement Cooperative*, *49*, 77–78.

Acosta-Gallegos, J. A., Kelly, J. D., & Gepts, P. (2007). Prebreeding in common bean and use of genetic diversity from wild germplasm. *Crop Science*, *47*(S3), 45–59. https://doi.org/10.2135/cropsci2007.04.0008IPBS

Balasubramanian, P., Vandenberg, A., Hucl, P., & Gusta, L. (2004). Resistance of *Phaseolus* species to ice crystallization at subzero temperature. *Physiologia Plantarum*, *120*(3), 451–457. https://doi.org/10.1111/j.0031-9317.2004.00257.x

Basu, P., Zhang, Y. J., Lynch, J. P., & Brown, K. M. (2007). Ethylene modulates genetic, positional, and nutritional regulation of root plagiogravitropism. *Functional Plant Biology*, *34*(1), 41–51. https://doi.org/10.1071/FP06209

Bates, T. R., & Lynch, J. P. (2000a). Plant growth and phosphorus accumulation of wild type and two root hair mutants of *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany*, *87*(7), 958–963. https://doi.org/10.2307/2656994

Bates, T. R., & Lynch, J. P. (2000b). The efficiency of *Arabidopsis thaliana* (Brassicaceae) root hairs in phosphorus acquisition. *American Journal of Botany*, *87*(7), 964–970. https://doi.org/10.2307/2656995

Bayuelo-Jiménez, J. S., Debouck, D. G., & Lynch, J. P. (2002). Salinity tolerance in *Phaseolus* species during early vegetative growth. *Crop Science*, *42*(6), 2184–2192. https://doi.org/10.2135/cropsci2002.2184

Beebe, S. E., Rao, I. M., Blair, M. W., & Acosta-Gallegos, J. A. (2013). Phenotyping common beans for adaptation to drought. *Frontiers in Physiology*, *4*, 1–20. https://doi.org/10.3389/fphys.2013.00035

Berny-Mier y Teran, J. C., Konzen, E. R., Medina, V., Palkovic, A., Ariani, A., Tsai, S. M., Gilbert, M. E., & Gepts, P. (2019). Root and shoot variation in relation to potential intermittent drought adaptation of Mesoamerican wild common bean (*Phaseolus vulgaris* L.). *Annals of Botany*, *124*(6), 917–932. https://doi.org/10.1093/aob/mcy221

Blair, M. W., Iriarte, G., & Beebe, S. (2006). QTL analysis of yield traits in an advanced backcross population derived from a cultivated Andean x wild common bean (*Phaseolus vulgaris* L.) cross. *Theoretical and Applied Genetics*, *112*(6), 1149–1163. https://doi.org/10.1007/s00122-006-0217-2

Blair, M. W., Wu, X., Bhandari, D., & Astudillo, C. (2016). Genetic dissection of ICP-detected nutrient accumulation in the whole seed of common bean (*Phaseolus vulgaris* L.). *Frontiers in Plant Science*, *7*, 1–9. https://doi.org/10.3389/fpls.2016.00219

Bonser, A. M., Lynch, J., & Snapp, S. (1996). Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytologist*, *132*(2), 281–288. https://doi.org/10.1111/j.1469-8137.1996.tb01847.x

Burak, E., Dodd, I. C., & Quinton, J. N. (2021). Do root hairs of barley and maize roots reinforce soil under shear stress? *Geoderma*, *383*, 114740. https://doi.org/10.1016/j.geoderma.2020.114740

Burridge, J. D., Rangarajan, H., & Lynch, J. P. (2020). Comparative phenomics of annual grain legume root architecture. *Crop Science*, *60*(5), 2574–2593. https://doi.org/10.1002/csc2.20241

Carminati, A., & Javaux, M. (2020). Soil rather than xylem vulnerability controls stomatal response to drought. *Trends in Plant Science*, *25*(9), 868–880. https://doi.org/10.1016/j.tplants.2020.04.003

Carminati, A., Passioura, J. B., Zarebanadkouki, M., Ahmed, M. A., Ryan, P. R., Watt, M., & Delhaize, E. (2017). Root hairs enable high transpiration rates in drying soils. *New Phytologist*, *216*(3), 771–781. https://doi.org/10.1111/nph.14715

Comas, L. H., Becker, S. R., Cruz, V. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. *Frontiers in Plant Science*, *4*, 16. https://doi.org/10.3389/fpls.2013.00442

Cortés, A. J., Monserrate, F. A., Ramírez-Villegas, J., Madriñán, S., & Blair, M. W. (2013). Drought tolerance in wild plant populations: The case of common beans (*Phaseolus vulgaris* L.). *PLOS One*, *8*(5), e62898. https://doi.org/10.1371/journal.pone.0062898

Dathe, A., Postma, J. A., Postma-Blaauw, M. B., & Lynch, J. P. (2016). Impact of axial root growth angles on nitrogen acquisition in maize depends on environmental conditions. *Annals of Botany*, *118*(3), 401–414. https://doi.org/10.1093/aob/mcw112

De Ron, A. M. (2015). Grain legumes. Vol.10. Springer.

Debouck, D. (1989). Early beans (*Phaseolus vulgaris* L. and *P. lunatus* L.) domesticated for their aesthetic value. *Annual Report of the Bean Improvement Cooperative*, *32*, 62–63.

Debouck, D. (1999). *Diversity in Phaseolus species in relation to the common bean. Common bean improvement in the twenty-first century*. Springer.

Debouck, D. G. (2000). *Biodiversity, ecology and genetic resources of Phaseolus beans - Seven answered and unanswered questions*. In K. Oono (Ed.), *Wild legumes* (pp. 95–123). Ministry of Agriculture, Forestry and Fisheries, and National Institute of Agrobiological Resources.

Fenta, B., Beebe, S. E., Kunert, K., Burridge, J., Barlow, K., Lynch, J. P., & Foyer, C. (2014). Field phenotyping of soybean roots for drought stress tolerance. *Agronomy*, *4*(3), 418–435. https://doi.org/10.3390/agronomy4030418

Freytag, G. F., & Debouck, D. G. (2002). *Taxonomy, distribution, and ecology of the genus Phaseolus (Leguminosae-Papilionoideae) in North America, Mexico and Central America*. Botanical Research Institute of Texas (BRIT).

Gahoonia, T. S., & Nielsen, N. E. (1998). Direct evidence on participation of root hairs in phosphorus (^{32}P) uptake from soil. *Plant and Soil*, *198*(2), 147–152. https://doi.org/10.1023/A:1004346412006

Ge, Z., Rubio, G., & Lynch, J. P. (2000). The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: Results from a geometric simulation model. *Plant and Soil*, *218*(1-2), 159–171. https://doi.org/10.1023/a:1014987710937

Gentry, H. S. (1969). Origin of the Common Bean, *Phaseolus vulgaris*. *Economic Botany*, *23*(1), 55–69.

Hacke, U. G., & Sperry, J. S. (2001). Functional and ecological xylem anatomy. *Perspectives in Plant Ecology Evolution and Systematics*, *4*(2), 97–115. https://doi.org/10.1078/1433-8319-00017

Hall, B., Lanba, A., & Lynch, J. P. (2019). Three-dimensional analysis of biological systems via a novel laser ablation technique. *Journal of Laser Applications*, *31*(2), 022602. https://doi.org/10.2351/1.5096089

Jochua, C. N., Strock, C. F., & Lynch, J. P. (2020). Root phenotypic diversity in common bean (*Phaseolus vulgaris L.*) reveals contrasting strategies for soil resource acquisition among gene pools and races. *Crop Science*, *60*(6), 3261–3277.

Kipe-Nolt, J. A., Montealegre, C. M., & Tohme, J. (1992). Restriction of nodulation by the broad host range Rhizobium tropici strain CIAT899 in wild accessions of *Phaseolus vulgaris* L. *New Phytologist*, *120*(4), 489–494. https://doi.org/10.1111/j.1469-8137.1992.tb01797.x

Klein, S. P., Schneider, H. M., Perkins, A. C., Brown, K. M., & Lynch, J. P. (2020). Multiple integrated root phenotypes are associated with improved drought tolerance in maize. *Plant Physiology*, *183*(3), 1011–1025. https://doi.org/10.1104/pp.20.00211

Kornegay, J. L., & Cardona, C. (1991). Inheritance of resistance to *Acanthoscelides obtectus* in a wild common bean accession crossed to commercial bean cultivars. *Euphytica*, *52*(2), 103–111. https://doi.org/10.1007/BF00021322

Kornegay, J., Cardona, C., & Posso, C. E. (1993). Inheritance of resistance to Mexican bean weevil in common bean, determined by bioassay and biochemical tests. *Crop Science*, *33*(3), 589–594. https://doi.org/10.2135/cropsci1993.0011183X003300030034x

Liao, H., Rubio, G., Yan, X., Cao, A., Brown, K. M., & Lynch, J. P. (2001). Effect of phosphorus availability on basal root shallowness in common bean. *Plant and Soil*, *232*, 69–79. https://doi.org/10.1023/A:1010381919003

Liao, H., Yan, X., Rubio, G., Beebe, S. E., Blair, M. W., & Lynch, J. P. (2004). Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. *Functional Plant Biology*, *31*(10), 959–970. https://doi.org/10.1071/FP03255

Lynch, J. P. (2011). Root phenes for enhanced soil exploration and phosphorus acquisition: Tools for future crops. *Plant Physiology*, *156*(3), 1041–1049. https://doi.org/10.1104/pp.111.175414

Lynch, J. P. (2013). Steep, cheap and deep: An ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany*, *112*(2), 347–357. https://doi.org/10.1093/aob/mcs293

Lynch, J. P. (2018). Rightsizing root phenotypes for drought resistance. *Journal of Experimental Botany*, *69*(13), 3279–3292. https://doi.org/10.1093/jxb/ery048

Lynch, J. P. (2019). Root phenotypes for improved nutrient capture: An underexploited opportunity for global agriculture. *New Phytologist*, *223*(2), 548–564. https://doi.org/10.1111/nph.15738

Lynch, J. P., & Brown, K. M. (2001). Topsoil foraging - An architectural adaptation of plants to low phosphorus availability. *Plant and Soil*, *237*(2), 225–237. https://doi.org/10.1023/A:1013324727040

Lynch, J. P., Chimungu, J. G., & Brown, K. M. (2014). Root anatomical phenes associated with water acquisition from drying soil: Targets for crop improvement. *Journal of Experimental Botany*, *65*(21), 6155–6166. https://doi.org/10.1093/jxb/eru162

Lynch, J. P., Mooney, S. J., Strock, C. F., & Schneider, H. M. (2021). Future roots for future soils. *Plant, Cell & Environment*, *In press*. https://doi.org/10.1111/pce.14213

Manschadi, A. M., Christopher, J., deVoil, P., & Hammer, G. L. (2006). The role of root architectural traits in adaptation of wheat to water-limited environments. *Functional Plant Biology*, *33*(9), 823–837. https://doi.org/10.1071/FP06055

Miguel, M. A., Widrig, A., Vieira, R. F., Brown, K. M., & Lynch, J. P. (2013). Basal root whorl number: A modulator of phosphorus acquisition in common bean (*Phaseolus vulgaris*). *Annals of Botany*, *112*(6), 973–982. https://doi.org/10.1093/aob/mct164

Miguel, M. A., Postma, J. A., & Lynch, J. P. (2015). Phene synergism between root hairs and basal root growth angle for phosphorus acquisition in common bean. *Plant Physiology*, *167*(4), 1430–1439. https://doi.org/10.1104/pp.15.00145

Miklas, P. N., Kelly, J. D., Beebe, S. E., & Blair, M. W. (2006). Common bean breeding for resistance against biotic and abiotic stresses: From classical to MAS breeding. *Euphytica*, *147*(1–2), 105–131. https://doi.org/10.1007/s10681-006-4600-5

Miller, C. R., Ochoa, I., Nielsen, K. L., Beck, D., & Lynch, J. P. (2003). Genetic variation for adventitious rooting in response to low phosphorus availability: Potential utility for phosphorus acquisition from stratified soils. *Functional Plant Biology*, *30*(9), 973–985. https://doi.org/10.1071/FP03078

Nabhan, G. P., Muruaga, M., Cardenas, R., & Burns, B. T. (1986). Wild bean explorations in northwest Mexico and southwest USA. *Plant Genetic Resources Newsletter*, *65*, 23–25.

Nestler, J., Keyes, S. D., & Wissuwa, M. (2016). Root hair formation in rice (*Oryza sativa* L.) differs between root types and is altered in artificial growth conditions. *Journal of Experimental Botany*, *67*(12), 3699–3708. https://doi.org/10.1093/jxb/erw115

Niklas, K. J. (1994). The scaling of plant and animal body mass, length, and diameter. *Evolution; International Journal of Organic Evolution*, *48*(1), 44–54. https://doi.org/10.2307/2410002

Nobel, P. S., & Jordan, P. W. (1983). Transpiration stream of desert species: Resistances and capacitances for a C-3, a C-4, and a CAM plant. *Journal of Experimental Botany*, *34*(147), 1379–1391. https://doi.org/10.1093/jxb/34.10.1379

Ochoa, I. E., Blair, M. W., & Lynch, J. P. (2006). QTL analysis of adventitious root formation in common bean under contrasting phosphorus availability. *Crop Science*, *46*(4), 1609–1621. https://doi.org/10.2135/cropsci2005.12-0446

Pachico, D. (1989). Trends in world common bean production. In H. Schwartz & M. Pastor-Corrales (Eds.), *Bean production problems in the tropics* (2nd ed., pp. 1–9). Centro Internacional de Agricultura Tropical.

Palta, J. A., Chen, X., Milroy, S. P., Rebetzke, G. J., Dreccer, M. F., & Watt, M. (2011). Large root systems: Are they useful in adapting wheat to dry environments? *Functional Plant Biology*, *38*(5), 347–354. https://doi.org/10.1071/FP11031

Pockman, W. T., & Sperry, J. S. (2000). Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany*, *87*(9), 1287–1299. https://doi.org/10.2307/2656722

Porch, T., Beaver, J., Debouck, D., Jackson, S., Kelly, J., & Dempewold, H. (2013). Use of wild relatives and closely related species to adapt common bean to climate change. *Agronomy*, *3*(2), 433–461. https://doi.org/10.3390/agronomy3020433

Purushothaman, R., Zaman-Allah, M., Mallikarjuna, N., Pannirselvam, R., Krishnamurthy, L., & Gowda, C. L. L. (2013). Root anatomical traits and their possible contribution to drought tolerance in grain legumes. *Plant Production Science*, *16*(1), 1–8. https://doi.org/10.1626/pps.16.1

Rangarajan, H., Postma, J. A., & Lynch, J. P. (2018). Co-optimization of axial root phenotypes for nitrogen and phosphorus acquisition in common bean. *Annals of Botany*, *122*(3), 485–499. https://doi.org/10.1093/aob/mcy092

Rao, I., Beebe, S., Polania, J., Ricaurte, J., Cajiao, C., Garcia, R., & Rivera, M. (2013). Can tepary bean be a model for improvement of drought resistance in common bean. *African Crop Science Journal*, *21*(4), 265–281. https://doi.org/10.4314/acsj.v21i4

R Core Team. (2016). The R Stats package. R Foundation for Statistical Computing.

Richards, R. A., & Passioura, J. B. (1989). A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain-yield in rain-fed environments. *Australian Journal of Agricultural Research*, *40*(5), 943–950. https://doi.org/10.1071/AR9890943

Rodriguez, M., Rau, D., Bitocchi, E., Bellucci, E., Biagetti, E., Carboni, A., Gepts, P., Nanni, L., Papa, R., & Giovanna, A. (2016). Landscape genetics, adaptive diversity and population structure in *Phaseolus vulgaris*. *New Phytologist*, *209*(4), 1781–1794. https://doi.org/10.1111/nph.13713

Rubio, G., Hong, L., Yan, X., & Lynch, J. P. (2003). Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. *Crop Science*, *43*(2), 598–607. https://doi.org/10.2135/cropsci2003.5980

Saengwilai, P., Chimungu, J., Rangarajan, H., Strock, C., Salungyu, J., & Lynch, J. P. (2021). Root hair phenotypes influence nitrogen acquisition in maize. *Annals of Botany*, *128*, 849–858. https://doi.org/10.1093/aob/mcab104

Shellie-Dessert, K., & Bliss, F. (1991). *Genetic improvements of food quality factors. Common beans: Research for crop improvement*. CAB International.

Singh, S. P. (2001). Broadening the genetic base of common bean cultivars: A review. *Crop Science*, *41*(6), 1659–1675. https://doi.org/10.2135/cropsci2001.1659

Singh, S. P., Cardona, C., Morales, F. J., Pastor-Corrales, M. A., & Voysest, O. (1998). Gamete selection for upright carioca bean with resistance to five diseases and a leafhopper. *Crop Science*, *38*(3), 666–672. https://doi.org/10.2135/cropsci1998.0011183X003800030008x

Singh Gahoonia, T., & Nielsen, N. E. (2004). Root traits as tools for creating phosphorus efficient crop varieties. *Plant and Soil*, *260*(1–2), 47–57. https://doi.org/10.1023/B:PLSO.0000030168.53340.bc

Singh, S., Nodari, R., & Gepts, P. (1991). Genetic diversity in cultivated common bean: 1. Allozymes. *Crop Science*, *31*(1), 19–23. https://doi.org/10.2135/cropsci1991.0011183X003100010004x

Sperry, J. S., & Ikeda, T. (1997). Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, *17*, 275–280. https://doi.org/10.1093/treephys/17.4.275

Sperry, J. S., & Saliendra, N. Z. (1994). Intra-plant and inter-plant variation in xylem cavitation in *Betula-occidentalis*. *Plant, Cell & Environment*, *17*(4), 1233–1241. https://doi.org/10.1111/j.1365-3040.1994.tb02021.x

Strock, C. F., Burridge, J., Massas, A. S. F., Beaver, J., Beebe, S., Camilo, S. A., Fourie, D., Jochua, C., Miguel, M., Miklas, P. N., Mndolwa, E., Nchimbi-Msolla, S., Polania, J., Porch, T. G., Rosas, J. C., Trapp, J. J., & Lynch, J. P. (2019b). Seedling root architecture and its relationship with seed yield across diverse environments in *Phaseolus vulgaris*. *Field Crop Research*, *237*, 53–64. https://doi.org/10.1016/j.fcr.2019.04.012

Strock, C. F., Burridge, J. D., Niemiec, M. D., Brown, K. M., & Lynch, J. P. (2021). Root metaxylem and architecture phenotypes integrate to regulate water use under drought stress. *Plant Cell and Environment*, *44*(1), 49–67. https://doi.org/10.1111/pce.13875

Strock, C. F., De La Riva, L. M., & Lynch, J. P. (2018). Reduction in root secondary growth as a strategy for phosphorus acquisition. *Plant Physiology*, *176*(1), 691–703. https://doi.org/10.1104/pp.17.01583

Strock, C. F., Schneider, H. M., Galindo-Castaneda, T., Hall, B. T., Van Gansbeke, B., Mather, D. E., Roth, M. G., Chilvers, M. I., Guo, X., Brown, K. B., & Lynch, J. P. (2019a). Laser ablation tomography for visualization of root colonization by edaphic organisms. *Journal of Experimental Botany*, *70*(19), 5327–5342. https://doi.org/10.1093/jxb/erz271

Tyree, M. T., & Ewers, F. W. (1991). The hydraulic architecture of trees and other woody plants. *New Phytologist*, *119*(3), 345–360. https://doi.org/10.1111/j.1469-8137.1991.tb00035.x

Tyree, M. T., Davis, S. D., & Cochard, H. (1994). Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction. *IAWA Journal*, *15*(4), 335–360. https://doi.org/10.1163/22941932-90001369

Vadez, V. (2014). Root hydraulics: The forgotten side of roots in drought adaptation. *Field Crops Research*, *165*, 15–24. https://doi.org/10.1016/j.fcr.2014.03.017

Vieira, R. F., Jochua, C. N., & Lynch, J. P. (2007). Method for evaluation of root hairs of common bean genotypes. *Pesquisa Agropecuaria Brasileira*, *42*(9), 1365–1368. https://doi.org/10.1590/S0100-204X2007000900020

Walk, T. C., Jaramillo, R., & Lynch, J. P. (2006). Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. *Plant and Soil*, *279*, 347–366. https://doi.org/10.1007/s11104-005-0389-6

Yao, Z., Zhang, W., Chen, Y., Zhang, W., Liu, D., Gao, X., & Chen, X. (2021). Nitrogen leaching and grey water footprint affected by nitrogen fertilization rate in maize production: A case study of Southwest China. *Journal of the Science of Food and Agriculture*, *101*(14), 6064–6073. https://doi.org/10.1002/jsfa.11263

York, L. M., Nord, E. A., & Lynch, J. P. (2013). Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science*, *4*, 355. https://doi.org/10.3389/fpls.2013.00355

Zhu, J., Kaeppler, S. M., & Lynch, J. P. (2005). Mapping of QTL controlling root hair length in maize (*Zea mays* L.) under phosphorus deficiency. *Plant and Soil*, *270*(1), 299–310. https://doi.org/10.1007/s11104-004-1697-y

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Massas, A. S. F., Strock, C. F., Schneider, H. M., Debouck, D. G., Brown, K. M., & Lynch, J. P. (2022). Comparative phenomics of root architecture and anatomy in *Phaseolus* species. *Crop Science*, *62,* 2347–2365. https://doi.org/10.1002/csc2.20838